REP 1990_023

Wildl. Soc. Bull. 18:282-290, 1990

RELATIVE VULNERABILITY OF COYOTES TO SOME CAPTURE PROCEDURES

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The protection of livestock and other commodities by capture and removal of coyotes (*Canis latrans*) is a common practice. Research to improve coyote capture methodology has included development and comparison of capture devices (Robinson 1943, Beasom 1974, Guthery and Beasom 1978, Linhart et al. 1981, Linhart et al. 1986, Olsen et al. 1986), development of toxicant delivery systems (Robinson 1948, Savarie and Sterner 1979, Connolly and Simmons 1984), and comparison of olfactory attractants (Turkowski et al. 1979, Bullard 1982, Fagre et al. 1983, Turkowski et al. 1983, Guthery et al. 1984).

Damage reduction is less effective if coyotes responsible for depredations are not vulnerable to the capture technique(s) used. However, there have been few assessments of differential bias among coyote capture procedures. For example, assumed biases toward capture of younger coyotes have not been measured, nor has the relative vulnerability to capture of territorial and transient (nonterritorial) coyotes been compared.

We examined capture data from previous studies to explore relative vulnerability by age, sex, and territorial classes of coyotes in relation to (1) capture methods, (2) spatial zones within coyote ranges, (3) duration of capture efforts, and (4) types of olfactory attractants.

STUDY AREAS AND METHODS

These analyses use coyote capture data from studies conducted in Webb County, Texas, between 1976 and 1986. Habitats on all sites are generally similar and representative of the South Texas Plains vegetational area (Gould 1975). Topography, soils, vegetation, climate, and land use were described by Windberg et al. (1985).

Capture data from 4 removal sampling procedures and 1 capture-release study were used and included coyote population samples obtained by (1) foothold traps, (2) M-44 devices (sodium cyanide ejectors; Matheny 1976), (3) shooting, and (4) collection of carcasses along highways. Details of procedures used to obtain each set of data follow.

Study I.—Coyotes were trapped each fall (Oct–Nov) and spring (Mar–Apr) from 1976 to 1986 to provide population samples for demographic estimates. Sampling areas ranged from 40 to 80 km^2 and were not resampled more frequently than every 4 years, with trapping periods ranging from 13 to 33 days ($\bar{x}$ = 23). We used No. 3 foothold traps with tranquilizer tabs (Balser 1965) containing 500 mg of propiopromazine hydrochloride (Diamond Laboratories, Des Moines, Ia.) and reset traps at the same site following captures of coyotes and other carnivores. Traps were distributed at densities of 0.7–1.5/km^2 and checked daily.

For comparing responsiveness of coyotes to olfactory attractants used at trap sets, we classed attractants into 3 categories: (1) coyote urine; (2) Carman's Canine Call Lure (CCCL; Russ Carman, New Milford, Pa.); and (3) other-lures (fetid materials from indigenous and novel animals, synthetic attractants, and other commercial lures). Use of specific attractants was discretionary, but frequency of use was generally similar among sample areas and periods.

Study II.—During 1977, 2 samples from the coyote population were obtained with M-44 devices in conjunction with studies of census methods. M-44's were set along a 45-km route in 5 separate transects, with 10 devices per transect spaced at 0.5-km intervals and ≥5 km between transects. A fetid lure, Mast's No. 6 (Frank Terry, Halfmoon Bay, Calif.), was used as the attractant on M-44s. During March and April, the M-44s were operated for 8 3-day periods, with 3-day pauses between periods. In October, 3 similar sampling periods were conducted.

Studies III and IV.—Two other samples were obtained from the coyote population in Webb County by checking 64 km of paved highway north and east of Laredo, Texas, every 2 days during October–November 1976 for carcasses of coyotes killed by automobiles and by shooting coyotes at night with the aid of predator calling devices for disease surveillance in October–November 1979.

Study V.— During 1984–1985, spatial use by female coyotes was studied on 2 areas (52 km^2 and 55 km^2) using radiotelemetry techniques. Methods for capturing and marking coyotes, collecting and analyzing data, and classifying territorial status of females were described by Windberg and Knowlton (1988). Specific capture procedures were comparable to Study I. We analyzed capture locations of territorial females in relation to their respective ranges by delineating 6 incremental spatial zones with the 45, 55, 65, 75, and 85% harmonic mean utilization contours of program HOME RANGE (Samuel et al. 1985); the zones define areas of potential use based on an approximation of the center of animal activity (Fig. 1). The ranges of transient (nonterritorial) females were delineated with the minimum-area method (Mohr 1947) in this analysis. We identified trap locations and coyote capture sites on aerial photographs (scale = 1:26,667) of the study areas and transcribed them to plots of coyote ranges in the same scale (Fig. 1). Analysis of capture locations in relation to coyote activity areas was restricted to ranges and territorial classifications determined within 3 months after capture.

An assessment of relative vulnerability to capture with traps was based on coyotes previously trapped, marked, and released in Study V. Only animals recaptured at locations and with olfactory attractants different from the initial capture were included in the analysis. Recapture rate was reported as the number of retrapped individuals/1,000 trap-days, with comparisons based on the cumulative number of trap-days with potential for recapture after release of each marked coyote.

Coyote age was estimated by relative pulp cavity size determined from radiographs of canine teeth (F. F. Knowlton and S. L. Whittemore, unpubl. data) and enumeration of cementum layers in microscopic sections of canine or premolar teeth (Linhart and Knowlton 1967). Adults were defined as >1 year and juveniles were ≤ 1 year. For some comparisons, the adult group was subdivided into adult (≥ 2.5 years) and second-year (1.5–2.0 years) age classes as in Windberg and Knowlton (1988).

We compared mean distance of capture sites from range boundaries for territorial and transient coyotes with unpaired t-tests. All other comparisons involved distribution of nominal data, which were analyzed by Chi-square contingency tables.

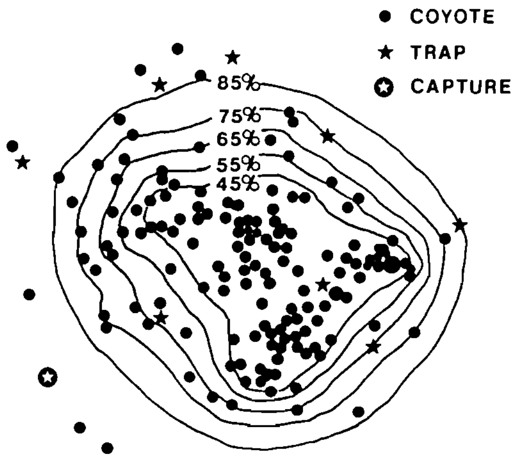

Fig. 1. Example of radiotelemetry locations (n = 196), harmonic mean utilization contour intervals (45, 55, 65, 75, and 85%) of the territorial range (Samuel et al. 1985), and trap and capture sites for 1 territorial female coyote.

RESULTS

Our analyses focused on differential biases of various capture procedures among age, sex, and territorial classes of coyotes. In addition, we assessed implications of territorial space to capture vulnerability of coyotes and potential differences in vulnerability associated with the duration of capture efforts. Comparisons were restricted to capture data within the same seasonal periods.

Relative Bias Associated with Capture Methods

Age classes of coyotes taken with traps and M-44 devices were compared using capture data from Studies I and II. In spring 1977, equal percentages (36%) of coyotes taken with M-44's (n = 196) and traps (n = 77) were juveniles. Likewise, percent juveniles among coyotes removed in fall 1977 did not differ significantly ($\chi^2 = 2.4$, 1 df, $P = 0.14$) between those taken with M-44's (39%, n = 54) and traps (54%, n = 52). Sex ratios of juveniles and adults taken with M-44's and traps were similar ($\chi^2 \leq 1.0$, 1 df, $P \geq 0.35$) in each season.

Juveniles composed a greater percentage ($\chi^2 = 10.7$, 1 df, $P < 0.01$) of coyotes killed by automobiles in Study III (71%, n = 49) than among those trapped for Study I (35%, n = 34) in fall 1976. Similarly, the percentage of juveniles among coyotes collected by shooting for Study IV (80%, n = 60) was greater ($\chi^2 = 21.8$, 1 df, $P < 0.01$) than among those trapped

Table 1. Percent distribution of area, capture effort, coyote capture sites, and radiotelemetry locations of coyotes in spatial zones for ranges of 26 territorial females as defined by harmonic mean utilization contours (Samuel et al. 1985), Webb County, Texas, 1984–1985.

Category	n	Zones defined by harmonic mean contours					
		≤45.0%	45.1–55.0%	55.1–65.0%	65.1–75.0%	75.1–85.0%	>85.0%
All coyotes							
Area within contours (km²)	44	29	11	14	18	27	
Capture effort (trap-days)	740	27	11	25	13	24	
Capture site[a]	52	21	12	33	8	27	
Territorial females[b]							
Radiotelemetry locations	26	61	8	8	7	6	11
Capture site	26	8	8	15	0	12	58

[a] Includes territorial females (n = 18, including 11 inside their respective ranges and 7 in territories of other females), transient females (n = 11), and unclassified males (n = 23).

[b] Mean percent distribution of radiotelemetry locations ($\bar{x}$ = 161) and capture sites for respective territory of each individual female.

for Study I (41%, n = 79) in fall 1979. Sex ratios did not differ ($\chi^2 \leq 1.0$, 1 df, $P \geq 0.36$) between coyotes killed by automobiles versus trapped or between coyotes shot versus trapped.

We compared recapture rates of coyotes marked and released as a measure of relative vulnerability to traps among sex, age, and territorial classes of coyotes. Of 155 marked coyotes with recapture potential, 30 were retrapped once and 4 were retrapped twice. By excluding coyotes retrapped at the same location or with the same olfactory attractant as their initial capture, we assumed that recapture rates represented an unbiased index of vulnerability to the method of capture (trapping) rather than differential learning about specific trap sets or attractants. The rates of recapture for males and females did not differ among adult (0.18 vs. 0.18), second-year (0.15 vs. 0.24) ($\chi^2 = 0.6$, 1 df, $P = 0.47$), or juvenile (0.13 vs. 0.42) ($\chi^2 = 1.7$, 1 df, $P = 0.19$) coyotes. Neither did the rate of recapture differ ($\chi^2 = 0.8$, 2 df, $P = 0.68$) among adult (0.18), second-year (0.19), and juvenile (0.27) coyotes (sexes combined) or between territorial (0.25) and transient (0.31) females ($\chi^2 = 0.2$, 1 df, $P = 0.69$).

We used data from Studies I and V (including recaptures) to assess whether the sex and age distributions of coyotes sampled by removal and mark-and-release trapping were comparable. In 1984 and 1985, percent juveniles among coyotes trapped on removal sites (27% of 71 and 16% of 67, respectively) and mark-release sites (23% of 93 and 22% of 85, respectively), using similar procedures, did not differ ($\chi^2 \leq 0.8$, 1 df, $P \geq 0.39$). Neither were male : female ratios of coyotes trapped on removal (31:40 and 32:35, respectively) and mark-release sites (43:50 and 41:44, respectively) different ($\chi^2 \leq 0.1$, 1 df, $P \geq 0.83$).

Vulnerability in Relation to Territorial Space

We compared coyote capture locations in relation to range boundaries by first assessing the distribution of trapping effort in relation to the territorial spatial zones delineated by program HOME RANGE (Fig. 1). The trapping effort was distributed among the zones in proportion to the area within each zone (Table 1). Because capture sites of coyotes were distributed similar to the trapping effort ($\chi^2 = 3.0$, 4 df, $P = 0.56$; Table 1), we conclude that territorial spacing did not preclude capture of coyotes throughout the study areas.

However, distributions of radiotelemetry locations and capture sites of individual territorial females in relation to spatial zones as-

Table 2. Percent juvenile coyotes trapped in relation to the duration of capture effort for removal and mark-release procedures, Webb County, Texas, 1977–1986.

Sequence of capture effort (days)	Removal trapping			Mark-release trapping		
	No. 5-day capture periods	No. captures	% juv.	No. 5-day capture periods	No. captures	% juv.
1–5	16	281	35	6	46	20
6–10	16	248	35	6	41	27
11–15	16	212	33	5	32	25
16–20	13	132	34	5	29	34
>20	7	76	33	3	24	29

Table 3. Percent of total captures among age and territorial classes of coyotes relative to length of time (days) individual traps were set, Webb County, Texas, 1982–1986.

Categories	*n*	No. days individual traps set			
		1–5	6–10	11–15	>15
Removal areas					
Adult	340	48	28	14	10
Juvenile	153	46	29	13	12
Mark-release areas					
Territorial female	32	54	34	9	3
Transient female	45	69	13	11	7

sociated with their respective territories differed significantly ($\chi^2 = 43.7$, 5 df, $P < 0.001$; Table 1). Among captures of 26 territorial females, only 2 (8%) occurred within the 45% utilization contour and 15 (58%) were outside the 85% contour of their respective territories. In contrast, a mean of 61% of their respective radiotelemetry locations were within the 45% contour and only 11% were outside the 85% utilization contour.

Nine of 12 transient females were captured outside the boundaries delineated for their respective ranges. Trapping efforts within the range boundaries of transient females ranged from 34 to 270 ($\bar{x} = 157$) trap-days. The mean distance that the 9 transients were captured outside their respective range boundaries was 0.3 km (range = 0.1–0.7 km), which did not differ ($t = 0.8$, 21 df, $P = 0.42$) from the mean distance of 0.4 km that 14 territorial females were captured outside the 85% utilization contour of their ranges (excluding 1 female captured 7.0 km outside). Two additional transient females were captured just 0.1 km inside their respective range boundaries.

Effects of Duration of Capture Effort

We assessed capture effort both from the beginning of capture periods and in relation to the time that individual trap sets were created because trapping regimes frequently involved increasing or moving traps. In the first instance, age bias toward the segment of the population with less strict site fidelity, presumably younger coyotes, might be expected as the removal effort becomes prolonged (e.g., ingress of transients following loss of territorial coyotes). However, percent juveniles among coyotes captured in each of 5 successive 5-day trapping periods (Studies I and V) was not different for either removal ($\chi^2 = 0.3$, 4 df, $P = 0.99$) or mark-release ($\chi^2 = 1.3$, 4 df, $P = 0.83$) procedures (Table 2).

In contrast, bias among the segment of the population that is most cautious (neophobic) might be associated with the tenure of individual trap sets. However, neither the percentages of juveniles and adults captured during removal trapping ($\chi^2 = 0.5$, 3 df, $P = 0.92$) nor the percentage of territorial and transient females captured during mark-and-release trapping ($\chi^2 = 5.0$, 3 df, $P = 0.19$) differed in relation to the number of days that individual traps were set (Table 3).

Relative Response to Olfactory Attractants

We found no sex-related differences ($\chi^2 \leq 1.4$, 1 df, $P \geq 0.24$) for coyotes captured using 3 types of olfactory attractants (Study I) among the season and age classes, except for more female than male juveniles captured in spring using other-lures ($\chi^2 = 4.4$, 1 df, $P = 0.04$). No seasonal differences in the distribution of

Table 4. Percent captures[a] using 3 types of olfactory attractants at trap sets in relation to age and territorial status of coyotes, Webb County, Texas, 1982–1986.

		Type of olfactory attractant		
Category	*n*	Coyote urine	CCCL	Other-lures
Removal areas:				
Fall:				
Adult	126	12	60	28
Juvenile	61	7	49	44
Spring:				
Adult	213	18	53	29
Juvenile	90	29	41	30
Mark-release areas:				
Territorial female	33	15	51	34
Transient female	45	24	37	39

[a] Percent captures of coyotes adjusted for relative number of trap-days/attractant in each period. Number of trap-days were: removal area (fall) = 2,701; removal area (spring) = 5,174; and mark-release area = 4,073.

adult captures among the 3 types of attractants were detected ($\chi^2 = 2.5$, 2 df, $P = 0.29$; Table 4). Among juveniles, however, proportionately more captures in spring resulted from using coyote urine than in fall ($\chi^2 = 5.1$, 1 df, $P = 0.02$), with correspondingly fewer captures attributed to other-lures ($\chi^2 = 5.3$, 1 df, $P = 0.02$).

The greatest percentage of adult coyotes were captured at trap sets with CCCL used as the olfactory attractant ($\chi^2 \geq 16.1$, 1 df, $P < 0.001$) and the least percentage where coyote urine was used ($\chi^2 \geq 6.5$, 1 df, $P < 0.001$; Table 4). The percentage of juvenile captures attributed to each of the 3 types of attractants did not differ in spring ($\chi^2 = 2.0$, 2 df, $P = 0.39$). In fall, however, fewer juveniles were captured using coyote urine than either CCCL ($\chi^2 = 13.7$, 1 df, $P < 0.001$) or other-lures ($\chi^2 = 12.3$, 1 df, $P < 0.001$). Overall (fall and spring), a greater percentage of adults than juveniles ($\chi^2 = 5.6$, 1 df, $P = 0.02$) were captured using CCCL than the other attractants.

In Study V, percent captures of transient females did not differ ($\chi^2 = 1.7$, 2 df, $P = 0.44$) among the 3 types of olfactory attractants (Table 4), but more territorial females were captured using CCCL than coyote urine ($\chi^2 = 5.0$, 1 df, $P = 0.03$). Among territorial females, 4 of 22 adults were captured with coyote urine as the attractant, whereas none of 11 young (1–2 years) females were caught using urine ($\chi^2 = 2.3$, 1 df, $P = 0.15$). Among 45 transient females, 4 of 12 adults and 4 of 33 young females were captured using coyote urine as the attractant ($\chi^2 = 2.7$, 1 df, $P = 0.10$). The percentage of adult and young individuals captured using CCCL and other-lures as attractants did not differ between territorial and transient females ($\chi^2 \leq 0.7$, 1 df, $P \geq 0.44$).

DISCUSSION

Our investigation of differential capture vulnerability was conducted in a region where coyotes are extremely abundant (Andelt 1985, Knowlton et al. 1986, J. R. Bean 1981. Indices of predator abundance in the western United States. U.S. Fish and Wildl. Serv., Denver Wildl. Res. Cent., Denver, Colo. 103pp.). The applicability of our interpretations to areas where coyotes are less abundant is conjectural.

Influence of Capture Procedures

Although coyote populations are commonly sampled by removal and mark-release procedures, information about relative sex and age biases between procedures is meager. Some differential bias between the 2 procedures might be expected; Andelt et al. (1985) reported relatively low scent-station visitations among coyotes previously subjected to intensive mark-release trapping and speculated that negative behavioral reinforcement associated with trapping may have affected their responses. Our results indicated that biases for age and sex did not differ between trapping for removal and mark-release purposes.

Coyotes killed by shooting at night with the aid of predator-calling devices and those killed by automobiles included more juveniles than coyotes captured with foothold traps and killed with M-44's. In an earlier report (Knowlton et al. 1986), we also noted that a small sample ($n = 12$) of coyotes shot from a helicopter in summer had a relatively high proportion of young (1–2 years) compared with a trapped sample. Differential capture rates were noted between seasons and age classes among the olfactory attractants used. Although we did not detect differences among the sex and age classes of coyotes taken with M-44's and traps, our comparisons may have been confounded by differences in olfactory attractants and areal deployment of the capture devices. Also, our data were derived from broad capture efforts directed at coyotes using specific study areas. It is conjectural whether similar results would be obtained by efforts directed toward specific individuals or smaller areas, as required to capture coyotes responsible for livestock depredations.

Selection and deployment of olfactory attractants are integral components of the capture process. Many of the relative biases to capture that we observed were presumably related to differential behaviors in response to the olfactory attractants used as lures with capture devices. We assume that urine scent evokes a behavioral response comparable to that of scent-marks by other coyotes (Kleiman 1966) and that our other 2 types of olfactory attractants arouse behavioral responses related to investigative (curiosity) or feeding urges (Bullard 1982). CCCL was classed separately because it has distinctive characteristics and consistently ranked high in previous comparisons of coyote attractants (Fagre et al. 1983, Turkowski et al. 1983). Our results indicate overall greater capture rates using CCCL as the attractant and also suggest that CCCL may be more effective for capturing adult and territorial coyotes. The increased attraction of juveniles to urine scent in spring compared to that in the preceding fall probably reflected physiological and behavioral maturation, which conforms with Quayle's (1983) observations regarding the ontogeny of urine-marking behavior among captive coyotes. She reported that marking by juvenile males increased significantly between October and the breeding period in spring.

Influence of Territorial Spacing

Hibler (1977) and Woodruff and Keller (1982) reported that most radio-collared coyotes were captured near the edge of or outside their normal ranges and postulated that coyotes might be more vulnerable to capture in less familiar areas. Harris (1983) demonstrated that captive coyotes readily investigated novel stimuli when encountered in unfamiliar environs but were neophobic to the same stimuli when encountered in familiar environments. His field studies showed that coyotes were more apt to visit scent stations peripheral to and outside their ranges than inside and suggested habituation was needed before coyotes investigated scent stations encountered within their normal areas of activity. His findings suggest that differential capture vulnerability might be associated with the length of time individual traps are set. Although our results unequivocally demonstrated decreased vulnerability to traps for both territorial and transient females in the interior of their respective ranges, we did not detect differential vulnerability between age classes associated with the length of capture effort nor between age or territorial status related to the length of time that individual traps were set. Either the initial removals of coyotes during 15–20 days were insufficient to alter age ratios of subsequent captures or the high coyote density (Knowlton et al. 1986) masked detection of any effect.

Although individual coyotes were less vulnerable to traps in the interior portions of their ranges than along the periphery, the distribution of coyote capture sites overall did not differ from that of trap locations within the study area. This suggests that capture efforts directed solely at coyote population reduction can disregard spacing patterns and range boundaries, whereas efforts to capture specific individuals might be more efficient if traps can be located along range boundaries. This conclusion differs from a preliminary interpretation (Knowlton et al. 1986) that all coyotes were less vulnerable in core areas of territories. The present analysis is more precise because more definitive procedures were used to delineate territorial spatial zones and capture data preceding the identification of territorial ranges were excluded. Our interpretations are consistent with data for coyote visitation at scent stations in relation to their ranges (Harris 1983). Although Laundre and Keller (1983) reported no association between capture sites and range boundaries, they did not provide the age and territorial status of the 9 coyotes they studied. At least 2 of the 4 coyotes they captured in central portions of ranges were juveniles (0.5 years). Roy and Dorrance (1985) snared (without use of attractants) as many resident coyotes ($n = 12$) within their ranges as along the periphery.

Our results indicating equal vulnerability to capture with traps among age and territorial classes are tenuous because the study areas were small (52–55 km²) in relation to the mean range size (12.4 km²) of transient coyotes (Windberg and Knowlton 1988). In that study we found that transient females, predominantly 1 and 2 years old, were located on the study areas only 55% of the time compared with 94% for territorial females (predominantly adults). Andelt (1985) reported that transient coyotes were located on his study area (32 km²) in southern Texas <50% of the time and that daily movements did not differ between territorial and transient coyotes. Assuming that relative exposure to traps is directly related to movement distances, individuals of the younger and transient classes may have been exposed to traps on the study areas significantly less than territorial coyotes. Hence, although the recapture rates derived in Study V were similar among age and territorial classes, the transient (and younger) individuals probably had only half the exposure to traps as did territorial adults, which suggests that they may be appreciably more vulnerable.

Overall, capture biases between sexes were not apparent among the data examined in this study. However, numerous differential biases associated with age, territorial status, responses to olfactory attractants, and the location of capture devices with regard to range boundaries were identified. We suggest that such behavioral differences might provide opportunities to improve the efficiency of coyote management programs by allowing capture strategies and perhaps other techniques to be directed at specific segments of coyote populations.

SUMMARY

Differential capture biases among age and territorial classes of coyotes were observed for some capture techniques. Coyotes killed with M-44 devices included similar proportions of juveniles and adults as coyotes captured using foothold traps. In contrast, juveniles composed greater proportions of coyotes killed by automobiles and collected by shooting at night compared with trapped coyotes. Similar sex and age ratios for coyotes trapped using removal and mark-release procedures suggested no differential sex or age biases associated with partial removals from populations. Evidence for greater trap vulnerability among young (1–2 years) and transient coyotes was implied because recapture rates were similar among all age and territorial classes although young and transient individuals probably had significantly less exposure to traps.

Territorial and transient females were seldom trapped within the interior of their ranges and were appreciably more vulnerable to capture along the edge of or outside their normal ranges. However, territorial spacing patterns did not preclude capture of other coyotes because capture locations of all coyotes did not differ from trap distribution.

Intensive trapping efforts on areas of 40–80 km^2 for 20 days did not alter the juvenile-adult ratio of subsequent captures. Compared with coyote urine and other-lures, CCCL was the most effective olfactory attractant for trapping adult and territorial coyotes.

Acknowledgments.—We thank H. L. Anderson, C. D. Mitchell, R. D. Roughton, W. M. Stephensen, and B. G. Wagner, Jr., for assistance in collecting coyotes. Specimens of coyotes collected by shooting were provided by staff of the Southeastern Cooperative Wildlife Disease Study. We greatly appreciate the radio-tracking assistance of D. L. LeCroy, C. D. Mitchell, E. W. Pearson, R. T. Sterner, K. L. Tope, B. G. Wagner, Jr., C. E. Wahlgren, and D. E. Zemlicka. R. E. Johnson and D. K. Steffen refurbished radio transmitters. M. Garcia provided radiography of coyote teeth. G. W. Smith and L. C. Stoddart assisted with data analysis. Numerous landowners cooperated by permitting access to private lands for the research; the following are acknowledged for providing access for extended periods: J. C. Martin, Jr., L. S. Murray, S. C. Scibienski, T. S. Scibienski, J. Van Cleve III, and G. S. Walker. We thank S. L. Beasom, M. J. Dorrance, R. M. Engeman, and L. C. Stoddart for comments on the manuscript. This study was conducted under the guidance and support of the U.S. Fish and Wildlife Service, U.S. Department of Interior. The Denver Wildlife Research Center transferred to the Animal and Plant Health Inspection Service, U.S. Department of Agriculture, on March 3, 1986. The Caesar Kleberg Wildlife Research Institute contributed financial support for this research. Identification of commercial products and companies does not constitute endorsement by the U.S. Government.

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Received 26 June 1989.
Accepted 14 March 1990.